EN ROUTE BEHAVIOR OF HOMING HERRING GULLS AS DETERMINED BY RADIO-TRACKING

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Problems associated with bird migration, spatial orientation, and navigation have stimulated considerable interest among biologists and others. During the last two or three decades increasing numbers of investigators have studied these problems, and their efforts have been greatly aided by the introduction of new sophisticated equipment and techniques. One of these recent approaches has been the application of radio-tracking equipment. This paper is the result of one attempt to use such equipment.

Prior to the availability of telemetry equipment, experimental birds were only observable at release times, possibly for a short period thereafter, and occasionally upon return. Seldom was it possible to determine the actual routes taken by homing birds or their apparent responses to environmental clues while en route. Exceptions to this statement are Griffin's and Hock's (1949) airplane tracking of Herring Gulls (*Larus argentatus*) and Gannets (*Morus bassanus*) and Hitchcock's (1952) and Griffin's (1952) airplane observations of pigeons (*Columba livia*). These data, however, were insufficient to indicate the procedures involved in avian homing.

During the summers of 1963 and 1964, I conducted orientation experiments with 50 adult Herring Gulls, 323 adult and subadult Ring-billed Gulls (*L. delawarensis*), 56 juvenile Ring-billed Gulls, and 294 Ring-billed Gull chicks from a colony near Rogers City (Presque Isle County), Michigan. My objectives were: (1) to examine the orientation requirements of each species; (2) to evaluate the homing and orientation abilities of both species; and (3) to determine the behavioral mechanisms and environmental factors associated with orientation as performed by these species.

METHODS

Adult Herring Gulls were captured with nylon snares, color-marked with alcohol soluble biological stains, and subjected to typical homing trials. During 1964, the gulls were anesthetized with Equitol (4.5 ml/kg) and transported to release sites in burlap bags. This paper pertains to one aspect of the study, the behavior of 41 Herring Gulls that were radio-tracked during homing flights from release sites located up to 110 miles from the colony (Table 1). Tracking distances for individual gulls ranged from 3 to 138 miles. Seven other gulls were equipped with transmitters but they were not tracked more than one mile because of transmitter failure, signal interference, or undetermined factors. The results discussed at this time are based on a total 1307 miles of radio-tracking and at least 285 radio-contact hours with experimental birds.

The radio-tracking equipment used during this study and some of the problems associated with the field application of this technique have been discussed previously (Southern, 1963, 1967). Two mobile units were used and each vehicle was manned by at least two

TABLE 1

SUMMARY OF RELEASE SITES AND SUCCESS RATES FOR RADIO-TRACKED HERRING GULLS.

	Distance of Release Sites from Colony							
	10 miles	20 miles	30 miles	40 miles	50 miles	60 miles	80 miles	110 miles
No. tracked	5	14	4	4	4	3	4	3
No. returned	5	8	4	3	3	2	2	2

41 tracked; 29 returned; success rate 70.8 per cent.

persons, a driver-receiver operator, and a recorder-map reader. One permanent station antenna was also maintained.

Twenty-nine (70.8 per cent) radio-tracked Herring Gulls returned successfully (Table 1) in periods ranging from 40 minutes (10 miles to release site) to 151 hours (30 miles). Eighteen of the 29 successful gulls were tracked during all, or most of their journey. The other returning individuals, and also those failing to home were tracked for periods ranging up to five hours. Their complete flights were not tracked for several reasons, e.g.: (1) a lack of adequate roads for use by tracking vehicles; (2) several gulls landed and remained at the same location for several hours and radio contact was eventually discontinued because of operator fatigue or other obligations; (3) prolonged flights by gulls in directions other than homeward resulted in the cessation of tracking operations; and (4) transmitter signals were lost as a result of human error, environmental factors, or equipment malfunction. Although several gulls were tracked over meandering routes of 100 or more miles, the farthest release site from which a gull's entire homing flight was tracked was 60 miles.

No attempt was made to initiate long-range trials since considerable information was available for Herring Gulls (Griffin, 1943; Matthews, 1952). I decided that the shorter trials, up to about 150 miles outside of the normal feeding range, would provide considerable data regarding the necessary environmental clues, homing success rates, and general orientation behavior. Results from such trials should also provide some information regarding the factors associated with orientation during longer flights by this species. Results from various studies tend to substantiate this contention (Kramer, 1961). Regardless of the type of homing study conducted, the conclusions which are drawn must always be restated in terms applicable to bird migration.

RESULTS

Flight patterns of successful homers.—Twelve (66.6 per cent) of the 18 Herring Gulls that were tracked for significant distances pursued south, east, or southeast courses during early flight periods, i.e., after initial departure. The other six gulls selected north (two), west (two), northeast (one), or southwest (one) as preliminary headings. The selected departure direction was often followed for a half mile or more before a change was made. In most cases (89 per cent), the initial heading was followed for about one-half mile and then it was altered by erratic or zigzag flight, with a half mile or less being flown in each of a variety of directions. In a few instances, a par-

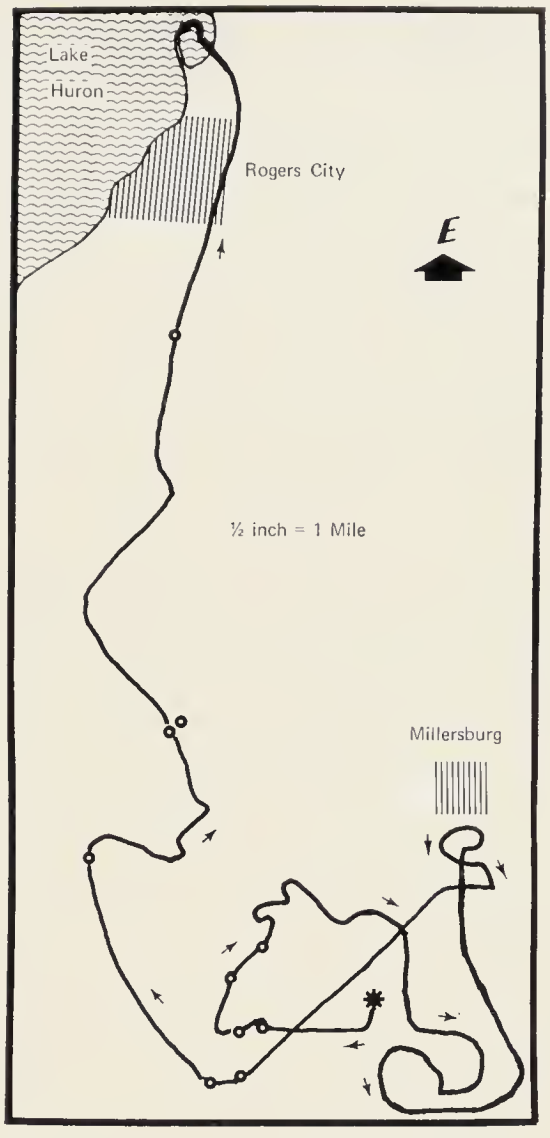

FIG. 1. Exemplary route of a radio-tracked Herring Gull released about 20 miles west of the colony. The colony is located on the peninsula east of Rogers City. Key to symbols: * = release site; o = period of circling behavior; → = direction of flight.

ticular route was maintained for about two miles before a different heading was selected. The fluctuating flight patterns involved as few as four headings and as many as 14. Repetition of easterly or southerly courses was common during prolonged periods of zigzag flight. Such behavior was occasionally interrupted by one or more circles that varied in diameter from a few yards to over one-half mile. The flight path of a Herring Gull tracked from its release site 20 miles west of the colony is illustrated in Figure 1. It is presented as a typical example of the type of information that was recorded for each homing flight.

The circling and erratic patterns were often followed by periods of straight flight which lasted for perhaps several miles. Ten (45.4 per cent) of the 22

Herring Gulls released between 10 and 30 miles west of the colony followed a course leading to some point on Lake Huron, usually Hammond Bay, which was located north of the colony and represented the nearest large body of water. Two of these gulls returned home promptly—in 40 and 50 minutes—from this point by routes over the water, but within one-half mile of the shoreline. The other eight birds spent extended periods of time on the water and occasionally made additional exploratory flights. These gulls required from 3 to 36 hours (average 17 hours) to return. A few individuals failed to return from this location and one gull, that was released 20 miles west of the colony, homed successfully without deviating its course toward Hammond Bay. It departed eastward, and pursued a fairly direct route to the colony after performing a few circles and zigzags. The entire flight required 50 minutes.

Twelve of the 22 Herring Gulls released up to 30 miles west of the colony departed along north, west, northwest, or northeast routes. Seven of the 12 returned in periods ranging from 3 to 151 hours (average 52 hours). Two gulls pursued northward courses toward a large inland lake (Black Lake) near Onaway. Both birds landed and remained on the lake for significantly long periods. Their courses between Black Lake and home were not determined, but one had a homing time of 85 hours, and the other 151 hours. In these instances, it seems that "incorrect" initial headings resulted in greatly increased average homing rates.

Individuals released at more distant sites, up to 110 miles, performed similarly with respect to general flight behavior. Only one Herring Gull was tracked during its complete homing flight from a site 60 miles from home. This bird was released near Little Traverse Bay (Emmet County) on Lake Michigan and spent six hours on the water preening, bathing, and just sitting. Thereafter, it flew southeast, zigzagged, circled, and then resumed a southeast course. This route was altered later and the gull followed a fairly direct path eastward to the colony. The flight lasted approximately two hours. Each gull released at locations along the other Great Lakes, or large inland lakes, reacted positively to these features and usually landed on the water. One of these birds returned from Lake Superior (110 miles from home) after I discontinued tracking operations following a three hour wait for its departure. It returned 21 hours later. A Herring Gull released 105 miles north-northwest, but inland from Lake Superior, followed an erratic course, changing directions 14 times in 12 minutes. Its flight path was not tracked for more than 20 minutes because roads were unavailable. This bird required 125 hours to return.

Gulls that successfully homed from distant locations exhibited the behavior patterns discussed in this section, but such activities were not unique to

successful individuals. Gulls that proved to be unsuccessful also zigzagged, circled, and altered their flight in other ways. There were, however, a few differences in flight patterns of the two groups and these will be discussed after I have described the remaining two categories.

Flight behavior of homing failures.—Six Herring Gulls failed to return from distances ranging up to only 30 miles from the colony. These individuals were tracked for distances totaling 170 miles and contact was maintained for about 45 hours. Only one of the six gulls departed on a southeasterly course. After circling and changing headings numerous times, it flew north-northeast to Hammond Bay. Its particular course headings were followed for various distances (e.g., 0.5, 1.0, 4.0, and 7.0 miles). One other gull from this group was tracked to Hammond Bay, but its original departure flight of 0.5 miles to the north was followed by turns to the east for 3 miles, north 10 miles, and finally northeast 4 miles to the Bay. It landed on the water, remained for a short time, and later flew parallel to the shoreline for about two miles toward the colony; however, it never returned. It seems unlikely that these two individuals would get this close to home and then be unable to find their way over the remaining distance. It is more likely that the gulls failed for other reasons, possibly because of a motivation loss (i.e., tendency change) which resulted from handling procedures during preparation for release. It is also possible, although unlikely, that both transmitters ceased to function after I left the birds at the above mentioned location and, as a result, I was unable to record their return.

The other homing failures in this distance category departed to the north, west, or northeast. One of these was tracked for 18 miles, to within seven miles of the colony, before contact was lost. The apparent failure of this bird to return might also be explained by one of the possibilities given previously, rather than by disorientation. The cause for loss of radio-contact was not determined.

There were six homing failures from distances ranging from 40 to 110 miles. Each individual circled and zigzagged soon after departure from release sites and two headed in homeward directions. The six gulls were tracked for 227 miles and for periods totaling 38 hours. In general, their behavior was comparable to that of birds failing to return from shorter distances.

Activities of delayed homers.—This discussion is not really distinct from the previous two topics. The behaviors described herein were also performed by members of the successful and unsuccessful groups.

Answers to several of the questions that continually occur during homing experiments may result from a knowledge of the activities and whereabouts of the birds that required, or took, unusually long periods of time to return from trials. Radio-tracking procedures enabled me to determine some pre-

liminary answers to these questions even though I was unable to continually follow all gulls that were equipped with transmitters. Three factors usually contributed to slow homing rates and to periods of extended absence: (1) extensive flights in non-homeward directions; (2) long periods spent in other than flight activity; and (3) hesitancy to enter the colony or increased wariness of the experimenter after return.

Several individuals were tracked for significant distances, up to 100 miles, in other than homeward directions. These flights might represent attempts to search for the familiar area or landmarks associated therewith, or they may be indicative of disorientation. The types of circling and zigzag patterns described previously were often repeated during such flights. These behaviors resembled the theoretical search patterns described by Griffin (1955). Searching, as recorded by radio-tracking, is not, however, as regular in pattern or as consistent in occurrence as those diagrammed by Griffin. It is interesting that many gulls eventually homed after flights of this nature; however, the factors associated with their eventual ability, or desire, to return were not determined. Radio-tracking data showed, at least in a few cases, that the eventual homeward flights were not direct, but usually involved zigzag patterns.

At least nine radio-tracked Herring Gulls landed in fields or on lakes and remained there for fairly long periods. Several untracked individuals behaved similarly. Occasionally these landings occurred immediately after release, particularly when gulls were freed near lakes or at night: but, on other occasions, the birds landed after traveling 15 or 20 miles. Recorded duration of such "rest periods" ranged from 15 minutes to 6 hours. It is possible that particular individuals remained even longer in one place since I usually discontinued tracking operations after the experimental subject remained at one location for three hours. "Rest sites" varied from lakes to open fields near release sites to similar areas located adjacent to the colony. Herring Gulls tracked along the south side of Lake Superior appeared attracted to flocks of local Herring Gulls whereas Herring Gulls released closer to home and Ring-billed Gulls released at all sites failed to show comparable tendencies. Several Herring Gulls spent at least three hours with these local groups of Lake Superior Gulls. There was no indication that this social attraction had any influence on orientation success. Gulls known to associate with local flocks required from 24 to 125 hours to return from a site 110 miles away.

The increased wariness of some individuals was mentioned earlier. Radio-tracking results showed that particular gulls spent several hours on the water or feeding near the colony prior to their actual return. Other birds returned. but were extremely nervous and departed when the observers approached.

Awareness of this type of behavior creates some concern regarding the accuracy of figures denoting homing success of non-tracked subjects used in this study and others.

Comparison between en route behaviors of successful and nonsuccessful Herring Gulls.—There were no obvious differences, of apparent significance, between en route flight behavior of successful and unsuccessful Herring Gulls. Both groups performed periodic circling and zigzag patterns which were interspersed with straight flights ranging up to 10 miles in length. A variety of temporary course headings (4 to 14) were followed by particular individuals of each group. Gulls released adjacent to large bodies of water usually landed. Birds that encountered lakes or open fields after departure from release sites also landed occasionally.

A few behavioral variations were apparent. The primary difference existed in departure directions. Approximately 68 per cent of the successful Herring Gulls departed to the east, south, or southeast which often represented the homeward direction. In contrast, only 25 per cent of the Herring Gulls that failed to return selected one of these three directions. This might seem to suggest that departure directions are indicative of homing ability; however, observational data failed to support this possibility. The other apparent behavioral difference pertained to the relative amounts of zigzagging. Successful gulls zigzagged less during homing flights. Several directions were pursued for various distances by the successful birds but the routine was not repeated as often nor did they pursue the number of different headings recorded for unsuccessful gulls. Several unsuccessful birds zigzagged for longer periods and performed this behavior in a much less regular fashion than did successful gulls. The homing failures sometimes changed course headings frequently, maintained new headings for shorter periods, and were likely to repeat these directions during the same zigzag sequence. The general impression was that of disorientation, or at least difficulty in selecting or maintaining a preferred course.

RESPONSE TO TOPOGRAPHICAL FEATURES

It is extremely difficult to evaluate accurately the role of landmarks in avian orientation. It appears almost impossible to determine by currently available techniques whether or not a bird is responding to specific topographic features. It is equally difficult to measure the extent of what might be considered a positive response to landmarks under field conditions. Regardless of this, many authors have reported various effects of landmarks (e.g., mountains, large bodies of water, valleys, shorelines) on homing birds. Matthews (1951, 1953, 1955) thought such features were used in landmark orientation; Graue and Pratt (1959), Hitchcock (1952, 1955),

Pratt and Thouless (1955), and Pratt and Wallraff (1958) believed they served as distracting factors; and others, Griffin (1952), Hitchcock (op.cit.), Arnould-Taylor and Malewski (1955), and Kramer (1957), have credited such features with having a type of funneling effect on birds. Schmidt-Koenig (1965), however, has pointed out that a good deal of evidence speaks against the role of landmarks in each of these three apparent responses. He feels that landmarks are certainly involved in recognition of home areas.

During this study it was occasionally possible to record the apparent reactions of gulls to particular gross land features (e.g., large bodies of water). If an experimental bird altered its course in accordance with particular landforms, this was considered as a positive response to that factor and that it is possibly involved in orientation.

Although radio-tracking techniques enabled me to determine the approximate route taken by homing birds, the method is not refined enough to accurately pinpoint a gull's position with relation to particular land features. The usual degree of plotting error encountered during triangulation on a transmitter-bearing gull's position would place the bird within a three- to six-acre area at a tracking range of about two miles. This error is further increased by the use of mobile units since the exact position of the vehicle cannot be determined. As tracking ranges decrease, as with landed birds or those meandering in one area for some time, tracking accuracy significantly increases. Even with maximum tracking efficiency, it is impossible to know the range of a bird's vision and to even postulate on the location of potential clues within the range of vision.

Because of these difficulties and others, it is obvious that no thorough evaluation of terrestrial clues has been conducted to date. Hochbaum's (1955) outstanding interpretation of waterfowl behavior probably represents the most thorough attempt. Until we possess a better understanding of avian learning, memory, and responses to particular land features, I consider it impossible to disregard the potential for birds using such features in long and short distance orientation.

In spite of these handicaps, it was possible to determine the reactions of radio-tracked Herring Gulls and color-marked Ring-billed Gulls to several types of gross land features. These were: (1) shorelines of the Great Lakes; (2) river valleys; (3) wooded moraines; and (4) roadways. More evidence was obtained regarding responses to shorelines since these features were most extensive and because it was easier to determine the bird's course in relation to these features.

A total of 69 gulls were released along the Great Lakes during the two years. Thirty-eight (55.1 per cent) returned successfully (Table 2). Seven of the Herring Gulls were radio-tracked for a total of 390 miles. Without

Table 2
Results of Homing Trials Associated With the Great Lakes.

Lake	Number released	Distance (miles)	Failed	Returned	Success per cent	Time range (hours)	Average
Michigan	13	68–82	7	6	46.2	16–29	26.2
Straits of Mackinac	8	55–60	1	7	87.5	7–28	20.1
Huron	17	15–17	9	8	47.1	2–88	38.5
Superior	31	85–150	14	17	54.8	19–92	43.1

exception, gulls released near one of the lakes followed the shoreline. In every case where the shoreline approximated a north-south direction and release sites were over 20 miles from home, a majority (78 per cent) of the gulls departed northward along the shore, regardless of homeward direction. Over half (56.8 per cent) of these birds failed to return. Gulls released at two localities, Lake Michigan (near Cross Village, Emmet County) and Lake Superior (north shore near Montreal River, Ontario), were all unsuccessful.

The activity of individuals released along the Lakes involved "resting" on the water but also periods of flight paralleling the shoreline. In many instances, these routes lead gulls farther from home. After I made several releases at particular sites, it was often possible to predict the outcome of the trials; i.e., most gulls departed northward along the shore and apparently required long periods to return or failed to return. Tracking records and observations of ring-bills suggested that they followed the shoreline in an attempt to locate familiar landmarks. The shoreline, although probably not visited previously by these individuals, resembled the home area and the typical situation a gull would normally frequent. The typical response to this situation was not suggestive of any ability to navigate or orientate by means of the sun or physical clues. The shoreline courses were followed for considerable distances in some cases and possibly until the desire to home was lost. It is also possible that these responses represent an attempt to select air currents suitable for flight. Updrafts would probably be associated with the Great Lakes shorelines and some moraines, and rising warm air from paved highways might effect low level flights. Therefore, response to these features might be related to flight dynamics and not to homeward orientation.

Two Herring Gulls released inland were tracked while they were apparently following the meandering course of the Ocqueoc River (Presque Isle County). Both birds followed the irregular non-homeward course of the river for about four miles. Thereafter, they headed on a more direct homeward course.

The river may have provided the necessary clues for selection of the latter course.

Only circumstantial evidence exists to support the speculation that Herring Gulls responded to moraines or highways. One individual was definitely observed to change its course to correspond with a north-south terminal moraine located about nine miles west of the colony. The west side of the forested hill was followed south for two miles before the gull angled eastward toward home. Several individuals appeared to follow roads during periods of low flight. They flew straight courses over the highway at elevations of 100 to about 200 feet and for distances ranging up to nine miles. While it seems unlikely that gulls could use individual roads as orientational clues outside of their familiar area, it is possible that the overall pattern of highways observable at high altitudes might influence flight direction during homing trials. Hochbaum (1955) referred to the use of various types of topographical features by waterfowl during flights within the familiar area. He also indicated the apparent use of similar clues during migration and showed that topographic configuration of the earth's surface channels flight in some areas. Further supportive evidence for use of landmarks was provided by Dorst (1963), Griffin (1952), (1955), Tinbergen (1949), and Wilkinson (1952). Griffin and Wilkinson have also demonstrated that these clues could be used in association with purely random search patterns. Skinner's (1950) work has provided additional support to this possibility by showing that the visual perception of pigeons is highly developed and would permit use of such clues. Skinner also found that pigeons possess visual memory and are able to respond to specific visual stimuli four years after the initial tests. Hamilton (1962), however, has suggested that these observations in themselves do not give evidence that features of the terrain establish the basic course of flight but only that passing birds respond to topography.

In general, it appears that a strong case still exists for landmark orientation by some species. However, so long as we must attempt to guess at what the bird might be seeing, recognizing, and responding to while en route, it will be impossible to adequately evaluate the role of topographical features in avian orientation.

SUMMARY

Forty-one Herring Gulls were radio-tracked during homing trials. Twenty-nine radio-tracked gulls returned successfully, 18 of which were tracked during essentially all of their flight. Initial flight behaviors were classified as direct, delayed, and those involving "rest periods." The flight patterns of successful, unsuccessful, and delayed homers are discussed.

Three factors contributed to slow homing rates: (1) flights in non-homeward directions;

(2) long periods involving other than flight behavior; and (3) hesitancy to actually enter the colony upon return.

Flight patterns of homing birds resembled the theoretical search patterns described in the literature. There were apparent responses in relation to particular topographical features, some of which could be predicted in advance by observers. Gulls followed shorelines of lakes, a river basin on one occasion, and a terminal moraine. Landmarks apparently influenced the direction of Herring Gull flight and may have played a role in orientation.

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NEW LIFE MEMBER

A recent addition to the roster of Life Members of the Wilson Ornithological Society is Dr. Richard C. Banks of Alexandria, Virginia. Dr. Banks, who holds degrees from The Ohio State University and the University of California, Berkeley, is currently Chief of the Bird Section. Bird and Mammal Laboratories, Division of Wildlife Research, Bureau of Sport Fisheries and Wildlife. His ornithological interests are in the systematics of North American birds, hybridization, and the biology of introduced birds, and he has published about 60 papers on birds and mammals. He is currently the Secretary of the A.O.U. and is also a member of the Cooper Society, the American Society of Mammalogists, Society of Systematic Zoology, and the Biological Society of Washington. Dr. Banks is married and has two children.